



THE UNIVERSITY *of* EDINBURGH

Edinburgh Research Explorer

Multilayer network analysis unravels haulage vehicles as a hidden threat to the British swine industry

Citation for published version:

Porphyre, T, Bronsvoort, M, Gunn, GJ & Correia-Gomes, C 2020, 'Multilayer network analysis unravels haulage vehicles as a hidden threat to the British swine industry', *Transboundary and Emerging Diseases*, vol. 67, pp. 1231-1246. <https://doi.org/10.1111/tbed.13459>

Digital Object Identifier (DOI):

[10.1111/tbed.13459](https://doi.org/10.1111/tbed.13459)

Link:

[Link to publication record in Edinburgh Research Explorer](#)

Document Version:

Peer reviewed version

Published In:

Transboundary and Emerging Diseases

General rights

Copyright for the publications made accessible via the Edinburgh Research Explorer is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The University of Edinburgh has made every reasonable effort to ensure that Edinburgh Research Explorer content complies with UK legislation. If you believe that the public display of this file breaches copyright please contact openaccess@ed.ac.uk providing details, and we will remove access to the work immediately and investigate your claim.





DR. THIBAUD PORPHYRE (Orcid ID : 0000-0002-8552-9899)

Article type : Original Article

Multilayer network analysis unravels haulage vehicles as a hidden threat to the British swine industry

Thibaud Porphyre^{1*}, t.porphyre@ed.ac.uk

Barend M. de C. Bronsvoort¹, mark.bronsvoort@roslin.ed.ac.uk

George J. Gunn², George.Gunn@sruc.ac.uk

Carla Correia-Gomes², Carla.Gomes@sruc.ac.uk

¹ The Roslin Institute, University of Edinburgh, Easter Bush Campus, Midlothian, Scotland

² Epidemiology Research Unit, Department of Veterinary and Animal Science, Northern Faculty, Scotland's Rural College (SRUC), Inverness Campus, Inverness, Scotland

*Corresponding authors: Dr. Thibaud Porphyre (Tel. +44 1483 232441; email: t.porphyre@ed.ac.uk);
ORCID: 0000-0002-8552-9899

Short title: Impact of haulage on infectious disease spread

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/TBED.13459](https://doi.org/10.1111/TBED.13459)

This article is protected by copyright. All rights reserved

Summary

When assessing the role of live animal trade networks in the spread of infectious diseases in livestock, attention has focused mainly on direct movements of animals between premises, whereas the role of haulage vehicles used during transport, an indirect route for disease transmission, has largely been ignored. Here, we have assessed the impact of sharing haulage vehicles from livestock transport service providers on the connectivity between farms as well as on the spread of swine infectious diseases in Great Britain (GB). Using all pig movement records between April 2012 and March 2014 in GB, we built a series of directed and weighted static multiplex networks consisting of two layers of identical nodes, where nodes (farms) are linked either by (1) the direct movement of pigs and (2) the shared use of haulage vehicles. The haulage contact definition integrates the date of the move and the duration Δs that lorries are left contaminated by pathogens, hence accounting for the temporal aspect of contact events. For increasing Δs , descriptive network analyses were performed to assess the role of haulage on network connectivity. We then explored how viruses may spread throughout the GB pig sector by computing the reproduction number R . Our results showed that sharing haulage vehicles increases the number of contacts between farms by >50% and represents an important driver of disease transmission. In particular, sharing haulage vehicles, even if $\Delta s < 1$ day, will limit the benefit of the standstill regulation, increase the number of premises that could be infected in an outbreak, and more easily raise R above 1. This work confirms that sharing haulage vehicles has significant potential for spreading infectious diseases within the pig sector. The cleansing and disinfection process of haulage vehicles is therefore a critical control point for disease transmission risk mitigation.

Keywords: epidemiology; network analysis; pigs; swine movement; infectious diseases; disease control

Introduction

Animal movement is recognised as an important route of transmission of diseases in livestock (Fèvre et al., 2006, Ortiz-Pelaez et al., 2006). As such, a wealth of research has been carried out to describe trade networks formed by the movement of livestock across Europe (Bajardi et al., 2011, Relun et al., 2016, Volkova et al., 2010). Understanding the complexity of the live animal trade network is critical to predict the spread of infectious diseases in livestock industries, assess the benefit of prevention and control measures and design cost efficient surveillance programmes. However, other mechanisms and relationships may indirectly connect farms to each other and represent additional routes of infection. Not accounting for these indirect contacts will lead us to underestimate the role of individual farms and limit the benefit of targeted strategies to control and prevent infectious diseases (Rossi et al., 2015, Bernini et al., 2019).

Livestock haulage and animal product transport vehicles have been shown as an important route of transmission for numerous infectious diseases. Ssematimba et al (2012) showed that the transport of shell eggs were the main mechanism of spread of highly pathogenic avian influenza virus (H7N7) during the 2003 epidemic in the Netherlands. Epidemiological links were also found between the routes taken by bulk milk tanker collectors and the spread of foot-and-mouth disease (FMD) virus during both the 1967-1968 UK and 1982 Denmark epidemics (Hedger and Dawson, 1970, Veterinærdirektoratet, 1982). With regards to the pig industry, transport vehicles played a major role in the transmission of classical swine fever (CSF) virus during the 1997-1998 outbreak in Netherlands (Elbers et al., 1999), accounting for more than half of the infection events before the implementation of the first control measures. Previously, contaminated vehicles have been shown as an important mechanism for the spread of African swine fever (ASF), porcine reproductive and respiratory syndrome (PRRS) and porcine epidemic diarrhoea (PED) viruses in both Europe and North America, mainly due to poor cleaning and disinfection practices of haulage vehicles between movements (Lowe et al., 2014, Dee et al., 2004a).

With regards to the study of pig trade networks, attention has mainly focused on networks formed by the direct movements of live animals between premises, with little consideration of the physical nature of such events. In particular, the successive use of a few livestock haulage vehicles by multiple farms to move animals will create additional contacts and increases the complexity of the animal trade network. To date, only few studies analyse animal trade networks looking at the role of indirect contacts by livestock haulage vehicles. Thakur and colleagues (Thakur et al., 2016) have extracted information on direct and indirect contacts that were voluntarily reported from 157 Canadian commercial pig farms within a 5-month period and showed that sharing lorries increased the connectivity of pigs farms. This result was further confirmed for similar networks looking at the role of intermediate transit movements of lorries between French farms without any animal unloading (Salines et al., 2017). Although these studies highlighted the potential role of

sharing livestock transport vehicles on the structure of the contact network between pig farms, none have formally assessed its potential impact for disease spread while, at the same time, accounting for the infectious period and contamination period of vehicles that are not only specific to pathogens but also are critical in defining infectious contact.

In this paper, we explore the changes in the structure of the live pig trade network in Great Britain (GB) when connections through potentially contaminated haulage vehicles are accounted for. Our goal is to assess the impact of haulage on the connectivity between farms and provide evidence on the risk posed by sharing haulage vehicles on the spread of infectious diseases in the British swine industry. In this study, we particularly focused on the impact of using private haulage companies (PHC) to transport pigs. These PHC are private livestock transport service providers commonly used in GB to move pigs both to slaughter or to non-slaughter premises (Porphyre et al., 2014).

Materials and Methods

Movement data

All movements reported between Monday 2nd of April 2012 to Sunday 30th of March 2014 were extracted from the Scottish livestock electronic identification and traceability database (ScotEID) and the electronic animal movement licensing system (eAML2) (Porphyre et al., 2017). Together, the ScotEID and eAML2 databases provide a comprehensive picture of all movements of pigs in GB at the batch rather than individual pig level. Each movement record reports the county/parish/holding (CPH) identifier for both departure and destination premises and the date on which the movement occurred. Details of premises type for departures and destinations are also recorded in the movement databases, allowing slaughterhouses, markets and other gathering places to be differentiated from agricultural holdings. In total, the pig trade network involves 34,812 holdings and 369 gathering places which moved in/off at least one pig within the study period in GB.

Over the entire dataset, the registration number of the vehicle used for transport showed poor quality in recording, whereas details on used haulier or haulage company were consistently provided. Hauliers and haulage companies recorded as transporting pigs were cross-checked against the list of quality assured private haulage companies (PHC) held by both Quality Meat Scotland (QMS) and Red Tractor. Together, a list of PHC that moved pigs during the study period was collated and provided details of each PHC, including their name, postcode and number of registered vehicles. This list was further extended by including all international haulage companies as well as all major live pig producers, major retail companies and genetic improvement (artificial insemination) businesses that showed records of using their

own fleet of haulage vehicles but were neither listed as PHC in the QMS nor in the Red Tractor datasets. In total, 863 PHC were identified as moving pigs in GB during the study period.

Network construction

To characterise the epidemiological relationship between pig premises through the trade of pigs in GB, we constructed a series of directed and weighted static multilayer networks between premises (whether agricultural holdings or gathering places) involved in the movement database. Here, each network is represented by two independent layers of “nodes” (Wasserman and Faust, 1994, Newman, 2002), where nodes represent premises involved in the movement of pigs, and in which each layer integrates the unique relationship between premises due to either the direct movement of pigs or sharing haulage vehicles (Figure 1A). Connections between nodes within each layer defined the intra-layer edges, whereas connections between nodes of different layers are the inter-layer edges (Figure 1A). Note that nodes involved in each layer represent the same entities (i.e. premises). As such, the combination of these two layers results in one multiplex network (Finn et al., 2019).

While contact definition is straightforward for the direct movement of pigs, with the contact $c_{ij}^M = 1$ from premises i to premises j if at least 1 pig has been reported moving in the movement database (and $c_{ij}^M = 0$ otherwise), defining contact through sharing haulage vehicles c_{ij}^H is complex. In this study, we only considered movements using PHC to transport pigs and ignored all movements that were carried out by vehicles owned by either the farm of departure or destination. Briefly, suppose that a batch of pigs moved from premises F_1 to premises F_2 at time t_1 and that another batch of pigs moved from premises F_3 to premises F_4 at t_2 (Figure 1B). Farms F_1 , F_2 , F_3 and F_4 would potentially be in contact if (1) both movements were carried out using the same PHC vehicle, and (2) the PHC vehicle that they share is contaminated, thereby carrying fomites (if not cleansed) and/or acting as a fomite (if not disinfected). As such, assuming PHC vehicles are constantly contaminated for a period Δ_S , F_1 , F_2 , F_3 and F_4 would be in contact if $t_2 - t_1 \leq \Delta_S$, i.e. both movements occurred within Δ_S . More formally, node i and node j would be in contact if both share a PHC vehicle to move pigs within Δ_S , such as $c_{ij}^H = 1$ if $0 < t_j - t_i \leq \Delta_S$, and $c_{ij}^H = 0$ otherwise. Note that, in this case, $t_j - t_i$ is required to be positive for a contact to occur, implicitly providing information on the direction of the contact (Figure 1B). However, a PHC vehicle may move multiple batches of pigs in the same day. Because only the date of the move is recorded in the movement database, with no information of the time of such a move, the direction of the contact may not be possible to establish. To solve this issue, the direction of all movements occurring in the same day, i.e. when $t_j - t_i = 0$, was randomly chosen with equal probability.

As noted previously, the registration number of the vehicle used for transport was poorly recorded in the movement database. Although we know which PHC was used for transporting pigs, we do not know

exactly which vehicle was used. While this is the same information for companies registered with a single vehicle, some companies may show records of >1 haulage vehicle. We therefore randomly allocated a vehicle to each movement with an equal probability and as a function of the number of vehicles registered per PHC. However, $<5\%$ of the PHC identified as moving pigs did not show records of number of vehicles. To infer missing records, we assumed that missing information was missing completely at random and represented a random subset of the data. We then imputed the missing number of vehicles by considering the number of vehicles registered per PHC is related to the \log_{10} -transformed average number of batches and the \log_{10} -transformed average number of pigs that were recorded moved by each PHC over all active days. This relationship was modelled using a multivariable Poisson regression model and developed in the statistical software R version 3.4.4 (R Development Core Team, 2018). The final model's Nagelkerke pseudo- r^2 was 0.536. Not only did this model allow the imputation of missing values, but it also enabled assessment of the number of vehicles required per PHC as according to their daily activities by evaluating the concordance between observed and predicted number of vehicles. Because we predicted the number of vehicles based on the number of batches and animals transported daily, we assumed that predictions would represent a benchmark of the number of vehicles required by each PHC given their daily activities within the pig sector. As such, PHCs that report a significantly smaller number of vehicles than the predictions from the Poisson model would have registered less vehicles than what it would be needed to carry out their daily activities, therefore highlighting that it would carry out multiple loads of pigs in a given single day.

Finally, both layers of the multilayer network were constructed by aggregating the recorded contact activity of each node over a given time-window Δt (Bajardi et al., 2011). In this process, we excluded slaughterhouses ($<0.5\%$ of the nodes) from the networks as we focus on disease spread between farms, though we retained their impact when defining c_{ij}^H . This provided a series of static multilayer networks for which edges connecting node i to node j are weighted by the number of batches $w_{ij}^M(t) = \sum_t^{t+\Delta t} c_{ij}^M(t)$ that were recorded moving within a given time period of length Δt (layer 1) and by the number of times $w_{ij}^H(t) = \sum_t^{t+\Delta t} c_{ij}^H(t, \Delta s)$ they share the same PHC vehicle within the same time period (layer 2). Overall, $Q = \lfloor 728/\Delta t \rfloor$ static multilayer networks were constructed for each value of Δt considered. In this study, $\Delta t = 7$ days and $\Delta t = 28$ days were considered for constructing networks, since these represent a range of likely farm-level infection period that would precede the detection of important swine diseases (such as ASF, CSF and FMD), thus preceding the implementation of disease control activities (Porphyre et al., 2017, Guinat et al., 2018). As such, for each scenario considered, 104 and 26 multilayer networks were constructed when $\Delta t = 7$ days and $\Delta t = 28$ days, respectively.

Network analysis and risk assessment

Here, we assumed that viruses can be transferred between premises in a similar way whether contact is direct or indirect. We further assumed that there is no cost to change layer (i.e., the relative weight of the inter-layers edges are all equal to 1) and that each layer represents an independent contact structure. As a result, the multilayer networks can be simplified by topological aggregate of the different layers. Although this assumption may fail in detecting fine-scale structural features of the networks (Battiston et al., 2014), such a loss is believed to have a limited impact on our inferences given the objectives of our study. Furthermore, such an assumption simplifies our analysis and allowed us to use methods developed for analysing and describing mono-layer networks rather than using more complex methods (Kivelä et al., 2014). Networks involved in each layer as well as the multilayer networks were therefore initially explored using classical descriptive network metrics, comparing the networks topology and size of the largest component and evaluating their vulnerability to targeted removals of premises when contacts due to sharing haulage vehicles is included rather than when only direct movement is considered.

Because, the duration of Δ_S varies as a function of the pathogen of interest (Lowe et al., 2014, Linhares et al., 2012, Dee et al., 2005a, Dee et al., 2005b, Dee et al., 2005c, Zimmerman et al., 2010, Weesendorp et al., 2008, Davies et al., 2017, Olesen et al., 2018) and as a function of the intensity of the cleaning activities carried out within the pig industry (Dee et al., 2005a, Dee et al., 2005b), we tested the impact of sharing PHC vehicles by considering various scenarios of Δ_S , notably $\Delta_S < 1$, $\Delta_S = 1$, $\Delta_S = 7$ and $\Delta_S = 28$ days. In total, 520 multilayer networks, which involved 1040 single-layer networks, were constructed and analysed. We then explored how diseases may spread between nodes of these multilayer networks and gain insight on the impact of sharing haulage vehicles on the between-farm basic reproduction number.

Network structure

First, the structure of each considered monolayer network was described using various network-level metrics and compared with those measured over the multilayer network. The topological measures computed describing the structure of the networks (Wasserman and Faust, 1994) included: the number of active nodes (n_n) and edges (n_e) involved in each network, the *density* (d ; the ratio of the observed number of edges to the number of possible edges) and the *average degree* (k ; the mean of the total number of edges, either incoming or outgoing, for each node). We also calculated the *average path length* (PL ; the average number of edges along the shortest paths between all pairs of nodes) and the *clustering coefficient* (CC ; the proportion of neighbours of a node that are linked to each other). A network is said to have a *small-world structure* if its CC is significantly higher, while at the same time showing a lower value of PL , than that computed from a random network of equivalent size and connections (that is with same number of nodes and links) (Humphries and Gurney, 2008). To evaluate if the pig trade network has a small-world structure

we computed the small-worldness index, S , which provide an unbiased comparison between the observed PL and CC with those computed for a set of randomly generated networks (Humphries and Gurney, 2008). Here, networks were considered having a small-world structure if $S \gg 1$ (Humphries and Gurney, 2008). For speed, and given that 1560 networks were constructed over the large number of considered scenarios and the study period, only 10 randomly generated networks were computed for computing the estimate of S for each empirical network.

We further calculated and analysed the distributions of the *in-degree* (k_{in} ; the number of different nodes from which a given node received contacts) and the *out-degree* (k_{out} ; the number of different nodes to which a given node sent contacts) for each node of the networks to explore how the connectivity of premises within each multilayer network vary with the considered scenario of Δ_S . We also computed the proportion of active nodes that were disconnected from the rest of the network in order to measure how indirect contact may affect the cohesiveness of the network. In this study, farms are considered disconnected if they did not receive or send pigs to other farms or gathering places. To further measure the impact of indirect contacts on the cohesiveness of the network, we then identified all nodes involved in the largest (or giant) weakly and strongly connected components. The *giant weakly connected component* (GWCC) of a given network is the largest subset of the network for which nodes can be reached from any other node by following edges regardless of their direction. The *giant strongly connected component* (GSCC) of a given network is, on the other hand, the subset of the network for which nodes can be reached from any other node by following directed edges. Based on these definitions, GSCC and GWCC can be considered independent from the rest of the network. These measures are also considered as proxy measures for lower and upper bounds of maximal epidemic size, respectively, for epidemics spreading in the considered network (Kao et al., 2006).

Finally, a percolation analysis was implemented to assess the vulnerability of the multilayer network to the targeted removal of premises (Min et al., 2014, Pilosof et al., 2017). Briefly, this analysis consisted of measuring the impact of progressively removing nodes, one after another, in the decreasing order of a given node centrality measure, on the structure of the network. Here, we measured the robustness of the structure of the multilayer network by measuring the impact of targeted removal of nodes on the sizes of the GSCC and GWCC when networks are constructed considering increasing values of Δ_S . Node centrality measures used in the analysis to drive the removal processes were k_{in} and k_{out} that were computed over the mono-layer network formed by direct movement alone. In this way, we can evaluate how sharing haulage vehicles may affect targeted removal strategies based on direct contact only.

Data were analysed using the 'igraph' (Csardi and Nepusz, 2006) and 'qgraph' (Epskamp et al., 2012) packages in the statistical software R version 3.4.4.

Disease reproduction number

To explore further how diseases may spread between nodes of the multilayer network, we extended the analysis by measuring the potential of each node to transmit pathogens to other nodes in the network. Disease transmission was assumed to only occur through direct movement of pigs and by sharing contaminated PHC vehicles; hence, we ignored the role of geographic proximity (Gamado et al., 2017) and returning haulage vehicles (Bronsvoort et al., 2008) on the spread of diseases. As such, we computed the probability $\Gamma_{ij}(q)$ that node j is infected due to contact with node i within the time period $q \in \{1, \dots, Q\}$ by considering that (1) susceptible nodes can be infected via either transmission routes simultaneously (Zhao et al., 2014) and (2) transmission follows a binomial process of the form:

$$\Gamma_{ij}(q) = 1 - (1 - \beta_M)^{w_{ij}^M(q)}(1 - \beta_H)^{w_{ij}^H(q, \Delta s)} \quad (1)$$

where $w_{ij}^M(q)$ and $w_{ij}^H(q, \Delta s)$ refer to the number of contacts from direct movements of pigs and through haulage contacts that occurred from i to j within q and considering a contamination period Δs , respectively. The parameters β_M and β_H further denote the probability that a node would infect another node as a result of sending a single batch of pigs or sharing a PHC vehicle, respectively. Therefore, these values differ from transmission rates from classical epidemiology models, which include contacts.

In Eq. (1), we assumed that the probability of pathogen transmission, $\Gamma_{ij}(q)$, varies between nodes due to their trading behaviour within a specific time period q . This makes a clear departure from the common hypothesis that transmission rates between individuals are constant, and implies that $\Gamma_{ij}(q)$ depends on specific edges. To comply with the common hypothesis of the homogeneous transmission, we neglected fluctuation and replaced $\Gamma_{ij}(q)$ by its mean value (Newman, 2002, Pastor-Satorras et al., 2015). In this way, the number of secondary cases that may be generated by each (potentially infectious) nodes i in a fully susceptible population during Δt may then be extrapolated by summing $\Gamma_{ij}(q)$ over all edges departing from i . As such, the average number of secondary cases over all node i can, therefore, be interpreted as a *de facto* approximation of the reproduction number R_q for diseases spreading in the multilayer, directed and weighted network constructed over the time period q . Like in mono-layer directed networks, the position of the node in which disease is introduced in a specific network component can restrict or enhance the spreading capabilities of the disease with respect to other positions (Pastor-Satorras et al., 2015). For example, incursion in small components will, in general, produce small outbreaks irrespective of the spreading rate, thus affecting our ability to generate an understanding of the macroscopic behaviour of an outbreak. To solve this issue, we focused our analysis on nodes involved in the largest strongly connected component (i.e., GSCC) (Pastor-Satorras et al., 2015), approximating the reproduction number R_q by:

$$R_q = \frac{1}{n_{GSCC}} \sum_{i \in GSCC}^{n_{GSCC}} \sum_j^N \Gamma_{ij}(q)$$

where N is the total number of premises recorded moving pigs in the movement databases; and n_{GSCC} is the number of premises involved in the giant strongly connected component of the multilayer network constructed over the time period q .

To investigate the dependence of β_M and β_H on the potential for given diseases to spread through the largest connected subset of multilayer network, we assumed that the infection process is constant over all Q time periods q within the study period and computed the mean R_q over the entire study period such as:

$$R = \frac{1}{Q} \sum_q R_q.$$

In this way, R represents an approximation of the basic reproduction number R_0 in the pig trade network in GB during the study period when accounting for the impact of sharing PHC vehicles, and can be interpreted similarly. A value of R greater than 1 indicates that disease will spread whereas a value of less than 1 indicates that a self-sustaining epidemic is not possible and that disease will die out (Anderson and May, 1991).

Sensitivity analysis

Acknowledging that network properties may have been influenced by how we constructed the haulage network (i.e. by randomly allocating vehicles and direction of edges), we evaluated the structural sensitivity of the multilayer network by constructing 100 multilayer networks over the movement data recorded over one randomly selected time-window Δt . Based on this set of 100 multilayer networks, we computed the distribution of the average degree k as well as the distributions of the in-degree k_{in} and out-degree k_{out} .

A stepwise regression analysis was further performed to determine which of Δt , Δs , β_M and β_H have the most impact on the variability of R . In this method, a sequence of linear regression models is constructed that successively adds the most important input parameters to the regression (Saltelli et al., 2000). The model difference in the coefficient of determination r^2 computed at each of the successive steps of the analysis provides then a measure of variable importance by indicating how much of the variation in the dependent variable can be accounted for. To avoid problems of non-linear relationships between the response and tested variables, rank-transformed variables were used in this analysis.

Results

Use of haulage in moving pigs

During the two-year study period, 415,448 batches of pigs were moved between the 35,181 active premises in GB, involving 32,820,599 pigs. Nearly 66% of these batches ($n=275,613$) moved to slaughter, which correspond to 51% of pigs ($n=16,777,608$) recorded in the database (Table 1). Overall, 41% of all movements and 33% of the non-slaughter movements were moved by a PHC, accounting for 83% and 78% of the moving pigs, respectively (Table 1). The distribution of distances travelled per batch of pigs in GB is shown in Figure 2A, highlighting long-distance movements were more likely to be made using PHC.

Figure 2B shows the distribution of the 863 PHC identified as moving pigs as a function of the total number of batches and pigs transported during the study period. While most of the 863 PHC were used to transport less than 10 batches ($n=489$; 57%) throughout the 24-month study period, large number of batches (i.e. >1000) were transported by only 43 (5%) PHCs (Table 2). The use of PHC is, however, not restricted to moving large batches of pigs (Fig. 1C), with half of PHCs transporting not more than a median of 4.5 pigs (95% range 1 – 249) per movement. In fact, Figure 2C suggests that two categories of PHC may be involved in moving pigs in GB: those that carry a median of 25 pigs or less per batch ($n=664$, named “small PHC”) and those that carry >25 pigs per batch ($n=199$, named “large PHC”).

Among the 863 PHC, 827 (96%) showed records of the number of vehicles used to transport animals. The comparison between the observed number of vehicles registered per PHC and the corresponding number of vehicles that was predicted based on their pig movements records (i.e. mean number of pigs and mean number of batches) is shown in Figure S1A. Considering that predictions represent a benchmark number of vehicles required by each PHC to move pigs given their daily needs, 190 of the 827 PHCs (23%) had significantly less vehicles than what would be needed, with 34 PHCs requiring >3 extra vehicles to move pigs as according to their daily recorded activities (Figure S1B). This highlights that these companies would carry out multiple loads of pigs in a given single day. In contrast, 127 of the 827 PHCs (15%) registered significantly more vehicles than required, with 9 PHCs registering >10 extra vehicles than needed to move pigs as according to their daily activities (Figure S1B). This highlights that these companies would probably carry other species than pigs. Nevertheless, PHC with a single registered vehicle moved fewer batches and fewer pigs than those with >1 registered vehicle (Tables 1 & 2). Figure 2D shows the distribution of the observed and predicted number of vehicles per PHC.

Impact of haulage on network topology

Here we are interested in evaluating how haulage may impact the topology of the pig trade network in GB and investigated how changes in the duration of the contamination period of a PHC vehicle (Δt) may

modulate this impact. This is particularly valuable as it gives us some indication of how diseases may spread in the population through the trade of pigs. The average estimates of the network topology measures for all generated static multilayer networks as well as for each layer (taken separately) are shown in Table 3 and Figure S2. Not surprisingly, increasing Δ_S yields larger network measures. In particular, increasing Δ_S grows the size of the network by 19% to 74% ($\Delta t=7$ days) and by 8% to 18% ($\Delta t=28$ days) in comparison to the network constructed over the direct movement of pigs only. However, it is worth noting that even sharing a PHC vehicle during the same day (i.e., $\Delta_S < 1$) has a major influence, not only increasing the size of the network but also increasing the number of edges, making the multilayer network markedly denser.

Focusing in the scenario $\Delta_S < 1$, farms will have 66% ($\Delta t=7$ days) to 91% ($\Delta t=28$ days) more contacts with other farms, increasing the average degree from 1.55 to 2.58 and from 1.89 to 3.62 when $\Delta t=7$ days and 28 days, respectively. The impact of sharing PHC vehicles on the network is further apparent in the distribution k_{in} and k_{out} computed over all considered Q time-windows and scenario of Δt and Δ_S (Figures 3A-B and S3A-B in Supporting information S1). Whether $\Delta t=7$ days or $\Delta t=28$ days, including haulage contacts was characterized by much broader distributions extending on all considered Δ_S . However, such an increase in contact was mostly felt on farms that have few contacts, i.e. those with $k_{in} < 5$ or $k_{out} < 5$, rather than those that have > 20 contacts (Supporting information S1, Figure S4). While these findings may have been sensitive to the assumptions used during the construction the haulage network (i.e. by randomly allocating vehicles and direction of edges), random allocation of vehicles and direction accounted for an absolute error of less than 0.2 (i.e. 3%) around the mean average degree of the pig trade network (Supporting information S1, Figure S5), with little impact on the general distribution (Supporting information S1, Figure S6). Hence, including the shared use of PHC vehicles in the pig trade network genuinely increased the general connectivity of premises.

As expected from the observed increased network density, including haulage contact in the pig trade network appears to reduce the proportion of farms that were recorded as moving pigs but did not receive or send pigs to other premises (Figure 3C and Figure S3C in Supporting information S1). Such a behaviour would happen if farms sent pigs exclusively to slaughter or if no movements have left the farms within the time windows. In the UK, stringent animal movement regulations were introduced nationwide following the outbreak of FMD in 2001, requiring a 20-day standstill period for all pigs on a farm upon the arrival of any new pigs onto that farm (i.e., no further movements of pigs off the farm in question are allowed for 20 days). This restriction¹ is intended to prevent substantial undetected spread of disease by isolating the farm from the rest of the industry long enough for disease to be clinically apparent and detected. However, our

¹ as regulated by the Disease Control Order 2003, statutory instrument (S.I.) S.I. 2003/1729 in England and the Welsh S.I. 2003/1966 in Wales; and The Disease Control (Interim Measures) (Scotland) Amendment (No. 3) Order 2007, Scottish S.I. (S.S.I.) 2007/423 in Scotland.

results show that sharing haulage vehicles would reduce the benefit of the 20-day standstill period and, hence, significantly increase the size of both giant weakly (GWCC) and strongly (GSCC) connected components present in all considered Q time-windows (Figures 3D & S3D). Whether alone or together with animal movement contacts, haulage contact drastically increases the size of the GSCC to a size similar to the GWCC computed when haulage is not included, even with a minimum period of contamination (i.e., $\Delta_S < 1$). On average, including haulage contact with $\Delta_S < 1$ day yields an 11- to 22-fold increase in the size of the GSCC, involving 7.8% ($n=154$) to 26% ($n=1284$) of the premises recorded moving pigs within $\Delta_t=7$ days and $\Delta_t=28$ days, respectively (Table 4). As Δ_S increases, however, more nodes are progressively included in the GSCC, gathering around 40% to 60% of the nodes involved in the multilayer network when $\Delta_S=28$ (Table 4). Interestingly, >80% of the nodes present in the GSCC report only using large PHC (i.e. moving batches of 25 more pigs, on average; Supporting information S1, Table S1), with little changes between networks constructed with $\Delta_t=7$ days and $\Delta_t=28$ days and for increasing Δ_S . Looking more in detail, these premises are mostly (60% to 68%) commercial producers. In contrast, 1.3% to 14% of the nodes present in the GSCC did not use PHC to move pigs at any moment during the study period (Supporting information S1, Table S1).

Results of the percolation analysis on the size of the GSCC when $\Delta_t=28$ days are shown in Figure 4 and Figures S7 in Supporting information S1. As expected, targeted removal of nodes in the order of k_{in} and k_{out} resulted in a fast reduction in the size of both GSCC and GWCC for all mono-layer networks constructed over the direct movement of pigs only. However, removing the targeted nodes will have a smaller impact on the multilayer network structure than when considering the monolayer network of direct contact alone. While removing 300 of the most central nodes, as defined by k_{in} , reduced the size of the GSCC by a median of 87.5% (IQR: 81% - 97%) and the size of the GWCC by a median of 97% (IQR: 96% - 98%), this only reduced the size of the GSCC by 40.9% (IQR: 0.427 - 0.382), 27.1% (IQR: 26% - 28) and 19.1% (IQR: 18% - 20%) when $\Delta_S < 1$ day $\Delta_S=1$ day and $\Delta_S=7$ days, respectively (Figure 4). A similar pattern can be seen when removing nodes in order of k_{out} (Figure S7 in Supporting information S1) and when $\Delta_t=7$ days (Figure S8 in Supporting information S1).

Impact of haulage on disease spread

Whilst the size of GSCC and GWCC provide clues on the upper limit in the number of farms infected in disease outbreaks (Kao et al., 2006), they offer limited information for evaluating the potential for pathogens to spread and generate epidemics. To do so, we computed the average number of secondary cases R from all premises involved in the GSCC of each q th time-window considered in this study and for a contamination period Δ_S of 0, 1 and 7 days. Furthermore, we departed from the previous (extreme) assumption that disease transmission occurs if at least one (infectious) contact is received by a susceptible

farm (i.e. when $\beta_M=1$ or $\beta_H=1$) by varying transmission probabilities β_M and β_H over large ranges of values. Figure S9, in Supporting information S1, shows that R is most sensitive to haulage contacts, albeit through β_H and Δ_S . Sensitivity analysis confirms this impression, as variations in β_H and Δ_S account for 44.1% and 33.4% of the observed variance in R . In comparison, β_M and Δ_t accounted for only 2.8% and 9.7% of the observed variance.

When plotting the threshold values of the transmission probability due to either the direct movement of pigs (β_M^*) or to the shared use of PHC vehicles (β_H^*) that yields $R>1$ for increasing values of β_H or β_M , respectively, we observe that diseases will have extreme difficulties to spread and generate outbreaks in situations where transmission could only occur through direct movements (Figure 5). In fact, over all scenarios considering $\beta_H=0$, $R>1$ only when $\Delta_t=28$ days and $\beta_M > 0.75$ (Figures 5A & 5B). The same is however not true for diseases spreading only through haulage contact (i.e. $\beta_M=0$; Figures 5C & 5D); in that $R>1$ when $\beta_H \geq 0.33, 0.20$ and 0.09 for $\Delta_t=7$ days, and $\beta_H \geq 0.24, 0.12$ and 0.03 for $\Delta_t=28$ days if $\Delta_S < 1, 1$ and 7 days, respectively. Beyond these two extreme cases, a single extra day of contamination (i.e. from $\Delta_S < 1$ to $\Delta_S=1$) makes a huge difference when $\beta_M \leq 0.5$, by reducing the value of β_H^* by 17% to 40% when $\Delta_t=7$ days and 26% to 52% when $\Delta_t=28$ days (Figure 5).

Discussion

The role of haulage has been previously identified as an important route of transmission (Dee et al., 2004b), leading to multiple studies evaluating the impact of sharing haulage vehicles on livestock trade networks (Augusta et al., 2019, Thakur et al., 2016, Salines et al., 2017, Bernini et al., 2019). Although Bernini and colleagues highlighted the importance of considering indirect contacts when estimating the final size of infectious disease epidemics in livestock at regional level, little has been done to fully explore and quantify the associated risk of infectious disease spread at national level. In this study, we attempt to fill this gap using the British swine industry, the only industry in GB where detailed records on haulage usage is available. To do so, we constructed a series of independent, directed and weighted multilayer networks in which each layer represent a different contact structure between premises involved in trading pigs in GB, namely the direct movement of pigs and the shared used of haulage vehicles, not only accounting for the timing of these movements but also the duration in which haulage vehicles remain contaminated and, thus, able to infect pig farms.

Multilayer networks, where each layer of connectivity may relate to one single type of relationship, can be used to represent many complex systems more accurately than was previously possible and help differentiate the impact of these different relationships on the structural functionality of the network (Pilosof et al., 2017, Kivelä et al., 2014). Particularly, the multilayer approach offers an opportunity to

consider the multiple interactions between individuals, populations or species, thus expanding our understanding on how animals communicate or behave (Finn et al., 2019) and on how pathogens are transmitted (Silk et al., 2018). In the context of animal movement networks, the multilayer approach offers a more holistic and less biased understanding of the connection between farms by accounting for both direct and indirect contacts.

Due to the large volume of data considered, some simplifications were however required. In particular, the role of inter-layer edges was not considered when examining the structure of the networks. This assumes that there is no costs in moving between layers (Kivelä et al., 2014). In our context, this implies that indirect contacts would lead to a farm (*i*) being infected in a similar way to direct contacts, and (*ii*) transmit pathogens to other farms irrespectively of the transmission routes. In reality, pathogens from contaminated vehicles would need to overcome biosecurity procedures implemented on farm to infect pigs present on farm. Although it is likely that we missed detecting fine-scale structural features of the networks (Battiston et al., 2014), we attempted to limit such an impact by considering distinct transmission rates (i.e. β_M and β_H) when computing the reproduction number R . In this way, we believe that such a loss has a limited impact on our inferences. However, further analyses will be needed to explore the implications of inter-layer edges in the dynamics of infectious diseases in the British pig industry.

Nevertheless, our results showed that sharing livestock haulage vehicles increases the number of indirect contacts between farms by >50% and represents an important driver of disease transmission in British pig industry. In particular, successively using the same haulage vehicles will limit the benefit of the mandatory livestock movement restrictions that were introduced in the aftermath of the FMD epidemics to prevent substantial undetected spread of infectious diseases in GB (e.g. S.I. 2003/1729 and S.S.I. 2007/423), even if the contamination period of lorries is <1 day. In other words, potentially infected farms may still remain in contact with susceptible premises despite not moving pigs off for 20 days after bringing in new stock (i.e. following the 20-day standstill period regulation), if these susceptible premises successively used the same haulage vehicles to move pigs.

Unlike in other countries (such as Canada, the US or Denmark) where pig production is fully (or almost fully) integrated and compartmentalised, the pig industry in GB involved a large proportion (around 80%) of producers that can be categorised as small or backyard pig holdings (Porphyre et al., 2017). Although the non-commercial sector of the pig industry is regarded as a low risk for disease spread in GB, previous simulation studies have shown that widespread epidemics of infectious diseases (such as CSF) may still occur from incursions in this population (Porphyre et al., 2017) and can involve farms of all sectors of the industry (Porphyre et al., 2016). In addition, small producers have been reported moving pigs using PHC in Scotland, particularly when these movements involved commercial farms or large distances (Porphyre et

al., 2014). Therefore, successively using haulage vehicles to move pigs represent an opportunity for pathogens to spread between sectors of the industry and exacerbate transmission, allowing the disease to spread to potentially large number of farms (Figure 3D) and over wide geographic areas (Figure 2A), even when disease transmission through animal movement is mitigated.

The targeted removal of highly connected nodes is considered an effective method to identify high-risk premises where mitigation and prevention measures would be most efficient against the spread of infectious diseases (Bajardi et al., 2011). While these high-risk premises are typically identified over their records of animal movements, we found that the effectiveness of such a strategy is markedly reduced when sharing haulage vehicles is considered. These findings further reinforce the importance of reducing connections between premises via hauliers.

This can be achieved by following regulation and ensuring lorries are properly cleansed and disinfected (C&D) as soon as possible after unloading or at least before the vehicle is next used for carrying livestock (The Transport of Animals (Cleansing and Disinfection) (England) (No. 3) Order 2003, S.I. 2003/1724). Despite being regulated in the UK, effective C&D procedures of haulage vehicles has proved to be difficult to achieve in the pig industry due to logistical and economic constraints related to its 'just in time' supply chain, where all steps of the production (i.e. insemination, farrowing, weaning, growing, slaughter and processing, distribution and delivery to outlet) are very inter-dependent (Salvage and Kettlewell, 2013). Because proper C&D of vehicles represent delays in the production (and therefore increases in costs), transporters are led to shorten the time allocated for cleansing their vehicles or to apply suboptimal standards in C&D procedures, such as washing vehicles with water alone or with poor use of disinfectant (Salvage and Kettlewell, 2013). Concomitantly, the limited access to proper washing facilities, which are mainly located in slaughterhouses in GB, may have hampered the ability of transporter to implement thorough C&D between loads. These behaviours are not restricted to the UK and have been subject of concerns for pig industries worldwide (Thakur et al., 2017, Bigras-Poulin, 2007, Lambert et al., 2012). Indeed, washing alone (followed or not by disinfection) reduces the amount of debris and organic matter but cannot fully eliminate viruses (Dee et al., 2004a, Dee et al., 2005a, Dee et al., 2005b, Dee et al., 2004b). This represents an important threat for pig industries as it limits farmers' ability to evaluate the biosecurity risk of haulage vehicles entering their property. As such, without improving the separation of the loading and unloading areas from the main farm perimeter, allowing potentially contaminated haulage vehicles to enter will only lead to increase the likelihood of a given farm being infected.

It is worth acknowledging that, since 2011, extensive efforts have been carried out by the British pig industry to improve the washing infrastructure available to livestock vehicles across all abattoirs in GB. As a consequence, the level of cleanliness of livestock haulage vehicles has generally improved. However, the

recent outbreak of swine dysentery in the British industry, for which contaminated livestock haulage vehicles is an important route of transmission (Giacomini et al., 2018, Hampson, 2018), highlights that improvement are still required in some parts of the industry. Inadequate C&D procedures of haulage vehicles may still prevent disease spread if they yield a reduction in the value of β_H below the minimum threshold β_H^* required for pathogens to spread. The value of β_H^* is generally unknown since it not only depends on the biology of pathogens but also the specificities of the pig industry in which it is introduced. However, providing robust estimates of β_H^* for various pathogens could be an important piece of information for supporting industries in their efforts to improve C&D procedures of haulage vehicles, and, hence, increase resilience against infectious diseases and prevent industry-wide outbreaks.

Nevertheless, it is clear from our results that allowing vehicles to remain contaminated for long periods of time will significantly decrease the value of β_H^* . In fact, we have shown that one extra day in contamination of lorries will drastically reduce the value of β_H^* , enabling the transmission number R to rise above 1 more easily. This finding is consistent with a recent modelling study looking at the role of indirect contacts due to livestock transport vehicles on the spread of infectious diseases between dairy farms in Italy (Bernini et al., 2019). Furthermore, a recent study from Canada has highlighted that trucks will remain contaminated with PRRS overnight in more than half of the time if only washing practices (i.e. current C&D practices) are implemented (Thakur et al., 2017). It is therefore critical that strict C&D measures, combining the use of bespoke disinfectant and a drying procedure (Dee et al., 2004a, Thakur et al., 2017), are completed with each vehicle within 24 hours or before its next load, whichever is the soonest, to ensure the elimination of viruses, or any other pathogens, from PHC vehicles and limit their potential to contaminate farms for multiple days.

In this study, we measured disease spread by computing the average number of secondary cases generated by any given infected farms through both direct movement and sharing haulage vehicles. To do so, we not only assumed (1) that the probability Γ_{ij} of a given farm infecting another is directly related to the aggregated number of contacts (w_{ij}^M and w_{ij}^H) between these two farms over a period of either 7 days or 28 days, but also (2) that the transmission probability due to contact for each considered transmission route (β_M and β_H) will be constant overtime. As such, the timing of both the contact and the infection events were not considered. These may have a profound impact on the risk of diseases to spread in networks (Enright and Kao, 2018, Nickbakhsh et al., 2013), potentially overestimating the risk of disease transmission. Furthermore, numerous studies have shown that air temperature is an important factor influencing the risk of disease transmission through haulage, principally by prolonging the survival of pathogens on contaminated surfaces (Linhares et al., 2012, Lowe et al., 2014, Dee et al., 2002, Dee et al., 2005c, Cutler et al., 2011) or affecting drivers' behaviours when carrying out C&D protocols. Although the influence of

such an external factor, as well as the impact of its seasonal variation, on the transmission probability β_H still remains widely uncertain (and was therefore not considered in the present study), it only stresses further that more work is needed to properly assess the role of haulage on the risk of disease spread.

The main objective of this study was to evaluate the risk posed by sharing haulage vehicles on the spread of infectious diseases in the British livestock industry. However, we focused on the pig sector rather than on the livestock industry as a whole (i.e. involving cattle, sheep and poultry). Although this was mainly due to the gap in the availability of data in the UK related to the use of haulage companies across the other sectors, it was also due to the acute awareness of the risk posed by haulage vehicles for the pig sector and the urgency to prepare for the threat posed by the ASF in Europe and Asia. In addition, we showed that several PHC have more vehicles registered in quality assurance schemes such as QMS and Red Tractor than they would normally require to transport pigs daily in the UK (Figure S1). This finding suggests that PHC in the UK are not restricted to transporting a single species. In other words, a single PHC may be hired to move either cattle, sheep or pigs. While there are multiple field evidences showing that PHC use the same vehicles to transport both cattle and sheep, it is not known whether pigs are transported in vehicles that also transported cattle and/or sheep. However, if this is true, this highlight the potential for haulage to facilitate the spread of multiple host diseases such as FMD, regardless of the quality of the C&D procedures implemented to ensure good biosecurity standard between species.

In conclusion, this work confirms that sharing haulage vehicles has significant potential for spreading infectious diseases within the pig sector and should not be ignored when assessing pathways for disease transmission or when mitigating the risk of spread in GB. In particular, we have shown that focusing on the animal trade network, without accounting for the impact of the vehicles that are carrying out these movements, will markedly underestimate the risk of disease transmission. Efforts to improve cleansing and disinfecting procedures of haulage vehicles, through improved protocols and infrastructure, is therefore an important critical control point for preventing infectious diseases to spread in an industry.

Authors' contributions

Designed the study: TP. Collected the data: CCG, GJG; Collated and analysed the data: TP. Wrote the manuscript: TP, BMdCB, CCG. TP, BMdCB and CCG read, edited and approved the final manuscript.

Funding

This work was co-funded by AHDB-pork, through the project “Combined Spatial and Network Analyses of English Pig Movement Data with disease modelling”, and by the Scottish Government Rural and Environment Science and Analytical Services Division, as part of the Centre of Expertise on Animal

Disease Outbreaks (EPIC). BMdCB acknowledges receiving core strategic funding from the BBSRC (BB/J004235/1) and gratefully acknowledges their support and contribution to this work.

Data Availability Statement

The data that support the findings of this study are available from Scottish EID Livestock Traceability Research and the Agriculture and Horticulture Development Board (AHDB-pork). Restrictions apply to the availability of these data, which were used under confidentiality agreements. Data are available at www.scoteid.com and www.eaml2.org.uk with permission.

Acknowledgements

The authors gratefully acknowledge Scottish EID Livestock Traceability Research and the Agriculture and Horticulture Development Board (AHDB-pork) for providing, under confidentiality agreements, a copy of the Scottish Livestock Electronic Identification and Traceability database (ScotEID), and the Electronic Pig Movement System (eAML2), respectively. The authors also thank Quality Meat Scotland and Red Tractor for providing a list of the assured haulage companies.

Ethical Statement

Ethical approval: Not applicable. This research does not involve human participants and/or animals.

Conflict of interest: The authors declare no competing financial interests.

References

- Anderson, R. M. and R. M. May, 1991: *Infectious Diseases of Humans: Dynamics and Control*. Oxford Science, Oxford, UK.
- Augusta, C., G. W. Taylor and R. Deardon, 2019: Dynamic contact networks of swine movement in Manitoba, Canada: Characterization and implications for infectious disease spread. *Transboundary and Emerging Diseases*, doi: 10.1111/tbed.13220.
- Bajardi, P., A. Barrat, F. Natale, L. Savini and V. Colizza, 2011: Dynamical patterns of cattle trade movements. *PLoS One*, 6, e19869.
- Battiston, F., V. Nicosia and V. Latora, 2014: Structural measures for multiplex networks. *Physical Review E*, 89, 032804.
- Bernini, A., L. Bolzoni and R. Casagrandi, 2019: When resolution does matter: Modelling indirect contacts in dairy farms at different levels of detail. *PLOS ONE*, 14, e0223652.
- Bigras-Poulin, M. B., K. Mortensen, S. & Greiner, M., 2007: Relationship of trade patterns of the Danish swine industry animal movements network to potential disease spread. *Prev Vet Med*, 80, 143-165.

- Bronsvort, B. M. d. C., L. Alban and M. Greiner, 2008: Quantitative assessment of the likelihood of the introduction of classical swine fever virus into the Danish swine population. *Prev Vet Med*, 85, 226-240.
- Csardi, G. and T. Nepusz, 2006: The igraph software package for complex network research. *InterJournal, Complex Systems*, 1695, 1 - 9.
- Cutler, T. D., C. Wang, S. J. Hoff, A. Kittawornrat and J. J. Zimmerman, 2011: Median infectious dose (ID₅₀) of porcine reproductive and respiratory syndrome virus isolate MN-184 via aerosol exposure. *Vet Microbiol*, 151, 229-237.
- Davies, K., L. C. Goatley, C. Guinat, C. L. Netherton, S. Gubbins, L. K. Dixon and A. L. Reis, 2017: Survival of African swine fever virus in excretions from pigs experimentally infected with the Georgia 2007/1 isolate. *Transbound Emerg Dis*, 64, 425-431.
- Dee, S., J. Deen, D. Burns, G. Douthit and C. Pijoan, 2004a: An assessment of sanitation protocols for commercial transport vehicles contaminated with porcine reproductive and respiratory syndrome virus. *Canadian Journal of Veterinary Research*, 68, 208-214.
- Dee, S., J. Deen, D. Burns, G. Douthit and C. Pijoan, 2005a: An evaluation of disinfectants for the sanitation of porcine reproductive and respiratory syndrome virus-contaminated transport vehicles at cold temperatures. *Canadian Journal of Veterinary Research*, 69, 64-70.
- Dee, S., J. Deen, K. Rossow, C. Wiese, S. Otake, H. S. Joo and C. Pijoan, 2002: Mechanical transmission of porcine reproductive and respiratory syndrome virus throughout a coordinated sequence of events during cold weather. *Canadian Journal of Veterinary Research*, 232-239.
- Dee, S., M. Torremorell, B. Thompson, J. Deen and C. Pijoan, 2005b: An evaluation of thermo-assisted drying and decontamination for the elimination of porcine reproductive and respiratory syndrome virus from contaminated livestock transport vehicles. *Canadian Journal of Veterinary Research*, 69, 58-63.
- Dee, S. A., J. Deen, S. Otake and C. Pijoan, 2004b: An experimental model to evaluate the role of transport vehicles as a source of transmission of porcine reproductive and respiratory syndrome virus to susceptible pigs. *Canadian journal of veterinary research*, 68, 128-133.
- Dee, S. A., B. C. Martinez and C. Clanton, 2005c: Survival and infectivity of porcine reproductive and respiratory syndrome virus in swine lagoon effluent. *Vet Rec*, 156, 56-57.
- Elbers, A. R. W., A. Stegeman, H. Moser, H. M. Ekker, J. A. Smak and F. H. Pluimers, 1999: The classical swine fever epidemic 1997–1998 in the Netherlands: Descriptive epidemiology. *Preventive Veterinary Medicine*, 42, 157-184.
- Enright, J. and R. R. Kao, 2018: Epidemics on dynamic networks. *Epidemics*, 24, 88-97.

- Epskamp, S., A. O. J. Cramer, L. J. Waldorp, V. D. Schmittmann and D. Borsboom, 2012: qgraph: Network visualizations of relationships in psychometric data. *Journal of Statistical Software*, 48, 1-18.
- Fèvre, E. M., B. M. d. C. Bronsvoort, K. A. Hamilton and S. Cleaveland, 2006: Animal movements and the spread of infectious diseases. *Trends in Microbiology*, 14, 125-131.
- Finn, K. R., M. J. Silk, M. A. Porter and N. Pinter-Wollman, 2019: The use of multilayer network analysis in animal behaviour. *Animal Behaviour*, 149, 7-22.
- Gamado, K., G. Marion and T. Porphyre, 2017: Data-driven risk assessment from small scale epidemics: Estimation and model choice for spatio-temporal data with application to a classical swine fever outbreak. *Frontiers in Veterinary Science*, 4, 16.
- Giacomini, E., S. Gasparrini, M. Lazzaro, F. Scali, M. B. Boniotti, A. Corradi, P. Pasquali and G. L. Alborali, 2018: The role of transportation in the spread of *Brachyspira hyodysenteriae* in fattening farms. *BMC Veterinary Research*, 14, 10.
- Guinat, C., T. Porphyre, A. Gogin, L. Dixon, D. U. Pfeiffer and S. Gubbins, 2018: Inferring within-herd transmission parameters for African swine fever virus using mortality data from outbreaks in the Russian Federation. *Transboundary and Emerging Diseases*, 65, e264-e271.
- Hampson, D. J., 2018: Distribution and transmission of aetiological agents of swine dysentery. *Veterinary Record*, 182, 192.
- Hedger, R. S. and P. S. Dawson, 1970: Foot-and-mouth disease virus in milk: an epidemiological study. *Vet Rec*, 87, 186-188 passim.
- Humphries, M. D. and K. Gurney, 2008: Network 'small-world-ness': A quantitative method for determining canonical network equivalence. *PLOS ONE*, 3, e0002051.
- Kao, R. R., L. Danon, D. M. Green and I. Z. Kiss, 2006: Demographic structure and pathogen dynamics on the network of livestock movements in Great Britain. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1999-2007.
- Kivelä, M., A. Arenas, M. Barthelemy, J. P. Gleeson, Y. Moreno and M. A. Porter, 2014: Multilayer networks. *Journal of Complex Networks*, 2, 203-271.
- Lambert, M. E., J. Arsenault, Z. Poljak and S. D'Allaire, 2012: Epidemiological investigations in regard to porcine reproductive and respiratory syndrome (PRRS) in Quebec, Canada. Part 2: prevalence and risk factors in breeding sites. *Prev Vet Med*, 104, 84-93.
- Linhares, D. C., M. Torremorell, H. S. Joo and R. B. Morrison, 2012: Infectivity of PRRS virus in pig manure at different temperatures. *Vet Microbiol*, 160, 23-28.
- Lowe, J., P. Gauger, K. Harmon, J. Zhang, J. Connor, P. Yeske, T. Loula, I. Levis, L. Dufresne and R. Main, 2014: Role of transportation in spread of porcine epidemic diarrhea virus infection, United States. *Emerging Infectious Diseases*, 20, 872-874.

- Min, B., S. D. Yi, K.-M. Lee and K. I. Goh, 2014: Network robustness of multiplex networks with interlayer degree correlations. *Physical Review E*, 89, 042811.
- Newman, M. E., 2002: Spread of epidemic disease on networks. *Physical Review E*, 66, 016128.
- Nickbakhsh, S., L. Matthews, J. E. Dent, G. T. Innocent, M. E. Arnold, S. W. Reid and R. R. Kao, 2013: Implications of within-farm transmission for network dynamics: consequences for the spread of avian influenza. *Epidemics*, 5, 67-76.
- Olesen, A. S., L. Lohse, A. Boklund, T. Halasa, G. J. Belsham, T. B. Rasmussen and A. Bøtner, 2018: Short time window for transmissibility of African swine fever virus from a contaminated environment. *Transboundary and Emerging Diseases*, 65, 1024-1032.
- Ortiz-Pelaez, A., D. U. Pfeiffer, R. J. Soares-Magalhães and F. J. Guitian, 2006: Use of social network analysis to characterize the pattern of animal movements in the initial phases of the 2001 foot and mouth disease (FMD) epidemic in the UK. *Preventive Veterinary Medicine*, 76, 40-55.
- Pastor-Satorras, R., C. Castellano, P. V. Mieghem and A. Vespignani, 2015: Epidemic processes in complex networks. *REVIEWS OF MODERN PHYSICS*, 87.
- Pilosof, S., M. A. Porter, M. Pascual and S. Kéfi, 2017: The multilayer nature of ecological networks. *Nature Ecology & Evolution*, 1, 0101.
- Porphyre, T., L. A. Boden, C. Correia-Gomes, H. K. Auty, G. J. Gunn and M. E. J. Woolhouse, 2014: How commercial and non-commercial swine producers move pigs in Scotland: A detailed descriptive analysis. *BMC Veterinary Research*, 10, 140.
- Porphyre, T., L. A. Boden, C. Correia-Gomes, H. K. Auty, G. J. Gunn and M. E. J. Woolhouse, 2016: Using national movement databases to help inform responses to swine disease outbreaks in Scotland: the impact of uncertainty around incursion time. *Scientific Reports*, 6, 20258.
- Porphyre, T., C. Correia-Gomes, M. E. Chase-Topping, K. Gamado, H. K. Auty, I. Hutchinson, A. Reeves, G. J. Gunn and M. E. J. Woolhouse, 2017: Vulnerability of the British swine industry to classical swine fever. *Scientific Reports*, 7, 42992.
- R Development Core Team, 2018: *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Relun, A., V. Grosbois, J. M. Sánchez-Vizcaíno, T. Alexandrov, F. Feliziani, A. Waret-Szkuta, S. Molia, E. M. C. Etter and B. Martínez-López, 2016: Spatial and Functional Organization of Pig Trade in Different European Production Systems: Implications for Disease Prevention and Control. *Frontiers in Veterinary Science*, 3.
- Rossi, G., G. A. De Leo, S. Pongolini, S. Natalini, S. Vincenzi and L. Bolzoni, 2015: Epidemiological modelling for the assessment of bovine tuberculosis surveillance in the dairy farm network in Emilia-Romagna (Italy). *Epidemics*, 11, 62-70.

- Salines, M., M. Andraud and N. Rose, 2017: Pig movements in France: Designing network models fitting the transmission route of pathogens. *PLOS ONE*, 12, e0185858.
- Saltelli, A., K. Chan and E. M. Scott, 2000: *Sensitivity Analysis*. Wiley & Sons, Chichester, UK.
- Salvage, D. and P. Kettlewell, 2013: Effective cleansing of Livestock vehicles at UK pig abattoirs. Technical report to the Agriculture and Horticulture Development Board - Pig (AHDB Pork, former BPEX).
- Silk, Matthew J., Julian A. Drewe, Richard J. Delahay, N. Weber, Lucy C. Steward, J. Wilson-Aggarwal, M. Boots, David J. Hodgson, Darren P. Croft and Robbie A. McDonald, 2018: Quantifying direct and indirect contacts for the potential transmission of infection between species using a multilayer contact network. 155, 731.
- Ssematimba, A., A. R. W. Elbers, T. J. Hagenaars and M. C. M. de Jong, 2012: Estimating the per-contact probability of infection by highly pathogenic avian influenza (H7N7) virus during the 2003 epidemic in the Netherlands. *PLOS ONE*, 7, e40929.
- Thakur, K. K., C. W. Revie, D. Hurnik, Z. Poljak and J. Sanchez, 2016: Analysis of swine movement in four Canadian regions: Network structure and implications for disease spread. *Transboundary and Emerging Diseases*, 63, e14-e26.
- Thakur, K. K., C. W. Revie, D. Hurnik and J. Sanchez, 2017: Modelling contamination of trucks used in the shipment of pigs infected with porcine reproductive and respiratory syndrome virus. *Journal of Swine Health and Production*, 25, 183-193.
- Veterinærdirektoratet, D., 1982: *Report on the Eradication of Foot-and-mouth Disease on the Islands of Funen and Zealand, Denmark 1982*. Danish Veterinary Service.
- Volkova, V. V., R. Howey, N. J. Savill and M. E. J. Woolhouse, 2010: Sheep movement networks and the transmission of infectious diseases. *PLOS ONE*, 5, e11185.
- Wasserman, S. and K. Faust, 1994: *Social Network Analysis: Methods and Applications*. Cambridge University Press, Cambridge, UK.
- Weesendorp, E., A. Stegeman and W. L. Loeffen, 2008: Survival of classical swine fever virus at various temperatures in faeces and urine derived from experimentally infected pigs. *Vet Microbiol*, 132, 249-259.
- Zhao, D., L. Li, H. Peng, Q. Luo and Y. Yang, 2014: Multiple routes transmitted epidemics on multiplex networks. *Physics Letters A*, 378, 770-776.
- Zimmerman, J. J., A. C. Jacobs, J. R. Hermann, C. Munoz-Zanzi, J. R. Prickett, M. B. Roof and K. J. Yoon, 2010: Stability of porcine reproductive and respiratory syndrome virus at ambient temperatures. *Journal of veterinary diagnostic investigation : official publication of the American Association of Veterinary Laboratory Diagnosticians, Inc*, 22, 257-260.

Tables

Table 1. Number of movements and animals moved between pig farms, gathering places and slaughterhouses in Great Britain between April 2012 and March 2014. For comparison, number of movements and animals that were transported using private haulage companies (PHC) that have one or more than one registered vehicle were also given.

Information	All movements	Movements using PHC with 1 vehicle	Movements using PHC with >1 vehicle
Total number of movements	415,448	18,241 (4.4%)	153,664 (37%)
Total number of pigs	32,820,599	1,229,370 (3.7%)	26,109,859 (79%)
Number of movements to slaughter	275,613	13,350 (4.8%)	112,099 (41%)
Number of pigs sent to slaughter	16,777,608	675,514 (4.0%)	14,080,529 (84%)
Number of non-slaughter movements	139,835	4891 (3.0%)	41,565 (30%)
Number of pigs moved to non-slaughter premises	16,042,991	553,856 (3.4%)	12,029,330 (75%)

Table 2. Descriptive statistics of the total number of movements and animals transported per private haulage company (PHC) in Great Britain between April 2012 and March 2014. Descriptive statistics were also provided for movements using PHC that have one or more than one registered vehicle.

Information	All movements	Movements using PHC with 1 vehicle	Movements using PHC with >1 vehicle
Number of PHC	863	616	247
Median (Q1-Q3) number of movements per PHC ^a	7 (2 - 50)	4 (2 - 15)	87 (6 – 480)
Min-Max number of movements per PHC ^a	1 - 12,777	1 – 1921	1 – 12,777
Median (Q1-Q3) number of pigs moved per PHC ^b	32 (7 – 751)	17 (4 – 75)	3268 (58 – 51,973)
Min-Max number of pigs moved per PHC ^b	1 – 1,860,331	1 – 154,549	1 - 1,860,331
Number of PHC moving			
Less than 10 batches	489	417	72
Between 10 and 99 batches	216	156	60
Between 100 and 999 batches	115	42	73
1000 or more batches	43	1	42
Number of PHC moving			
Less than 10 pigs	274	242	32
Between 10 and 99 pigs	278	240	38
Between 100 and 999 pigs	106	74	32
Between 1000 and 9999 pigs	84	37	47
10,000 or more pigs	121	23	98

^a. Total number of movements carried out by each PHC during the study period.

^b. Total number of pigs moved by each PHC throughout the study period.

Table 3. Descriptive network statistics for each layer and the entire multilayer networks characterising pig movements in Great Britain between April 2012 and March 2014.

Networks	Δs	$\langle n_n \rangle$	$\langle n_e \rangle$	$\langle d \rangle$ (x1000)	$\langle k \rangle$	$\langle PL \rangle$	$\langle CC \rangle$	$\langle S \rangle$
$\Delta t = 7\text{days}$								
<i>Animal movement</i>	-	1668.7	1299.7	0.477	1.552	1.861	0.004	0.39
<i>Haulage contact</i>	$\Delta s < 1$	846.0	1465.2	2.055	3.456	7.390	0.486	7.34
	$\Delta s = 1$	1072.6	3328.3	2.888	6.184	8.244	0.465	1.28
	$\Delta s = 7$	1424.3	13795.9	6.776	19.312	4.998	0.499	0.29
	$\Delta s = 28$	1900.0	57043.0	15.680	59.726	3.481	0.569	0.14
<i>Both</i>	$\Delta s < 1$	1980.1	2547.6	0.667	2.576	8.823	0.242	14.72
	$\Delta s = 1$	2168.1	4385.5	0.953	4.049	8.244	0.364	8.11
	$\Delta s = 7$	2473.7	14795.0	2.459	11.986	5.198	0.481	1.28
	$\Delta s = 28$	2907.2	57968.9	6.962	39.983	3.697	0.565	0.19
$\Delta t = 28\text{days}$								
<i>Animal movement</i>	-	4605.2	4369.6	0.210	1.895	3.930	0.005	0.42
<i>Haulage contact</i>	$\Delta s < 1$	1631.8	5399.8	2.029	6.614	6.785	0.291	2.43
	$\Delta s = 1$	1748.0	10995.7	3.599	12.571	5.333	0.338	0.54
	$\Delta s = 7$	1906.8	34545.6	9.508	36.213	3.891	0.466	0.20
	$\Delta s = 28$	2214.6	90694.1	18.466	81.718	3.188	0.568	0.10
<i>Both</i>	$\Delta s < 1$	4979.0	8975.0	0.372	3.621	7.162	0.163	6.63
	$\Delta s = 1$	5066.5	14509.1	0.582	5.764	6.005	0.272	4.22
	$\Delta s = 7$	5194.4	37903.4	1.457	14.741	4.643	0.445	1.14
	$\Delta s = 28$	5454.6	93904.5	3.278	34.815	3.890	0.560	0.33

Δs : Contamination period; Δt : Aggregation time-window as an approximate for infectious period; $\langle n_n \rangle$: Mean number of active nodes in networks; $\langle n_e \rangle$: Mean number of edges in networks; $\langle d \rangle$: Mean density of the network; $\langle k \rangle$: Mean average degree observed in network; $\langle PL \rangle$: Mean average path length; $\langle CC \rangle$: Mean clustering coefficient; $\langle S \rangle$: Mean small-worldness index.

Table 4. Mean number of active nodes involved in the giant components for each layer and the entire multilayer networks characterising pig movements in Great Britain between April 2012 and March 2014.

Networks	Δs	$\Delta t = 7$ days			$\Delta t = 28$ days		
		$\langle \text{GSCC} \rangle$	$\langle \text{GWCC} \rangle$	%GS	$\langle \text{GSCC} \rangle$	$\langle \text{GWCC} \rangle$	%GS
<i>Animal movement</i>	-	13.5	211.9	0.81%	57.4	2339.4	1.25%
<i>Haulage contact</i>	$\Delta s < 1$ day	87.6	379.7	10.35%	1041.7	1491.4	63.84%
	$\Delta s = 1$ day	462.1	853.2	43.09%	1376.3	1656.8	78.74%
	$\Delta s = 7$ days	1164.4	1321.4	81.75%	1737.1	1821.5	91.10%
	$\Delta s = 28$ days	1747.5	1813.5	91.97%	2057.8	2117.9	92.92%
<i>Both</i>	$\Delta s < 1$ day	153.6	780.2	7.76%	1284.3	2965.0	25.79%
	$\Delta s = 1$ day	535.1	1239.5	24.68%	1559.0	3112.2	30.77%
	$\Delta s = 7$ days	1196.9	1692.4	48.38%	1868.5	3273.5	35.97%
	$\Delta s = 28$ days	1774.9	2184.2	61.05%	2188.8	3553.2	40.13%

Δs : Contamination period; Δt : Aggregation time-window as an approximate for infectious period; $\langle \text{GSCC} \rangle$

: Mean number of nodes involved in weekly (i.e. $\Delta t = 7$ days) or monthly (i.e. $\Delta t = 28$ days) giant strong components; $\langle \text{GWCC} \rangle$: Mean number of nodes involved in weekly (i.e. $\Delta t = 7$ days) or monthly (i.e. $\Delta t = 28$ days) giant weak components; %GS: Mean proportion of active farms involved in the giant strong component among all farms recorded moving pigs in the British pig trade network during the study period.

Figure legends

Figure 1. The multilayer contact network. (A) The network has two layers, representing the contact between premises through the direct movement of pigs, and through sharing haulage vehicles. Nodes (i.e. premises) in each layer represent the same entities. Here, intra-layer edges are depicted by solid lines while inter-layer edges are shown in dashed lines. (B) Toy example illustrating how connections are created in the haulers network. In (B), farms F1, F2, F3 and F4 are in contact if (rows) movements were carried out using the same vehicle, and if (column) the movement occurs within the contamination period Δs . Note that direction of the connection depends on the timing of the movements.

Figure 2. Description of the use of private haulage companies (PHC) in Great Britain between April 2012 and March 2014. (A) Comparison of the Euclidean distance travelled between premises when a PHC is used or not. (B) Distribution of PHC used as function of number w of batches or pigs transported. (C) Distribution of average batch size per PHC, (D) Distribution of the number of vehicles per PHC. In (D), the number of vehicles were either provided from records or inferred from linear interpolation of the records based on the mean daily number of batches and pigs for each PHC recorded in the movement database.

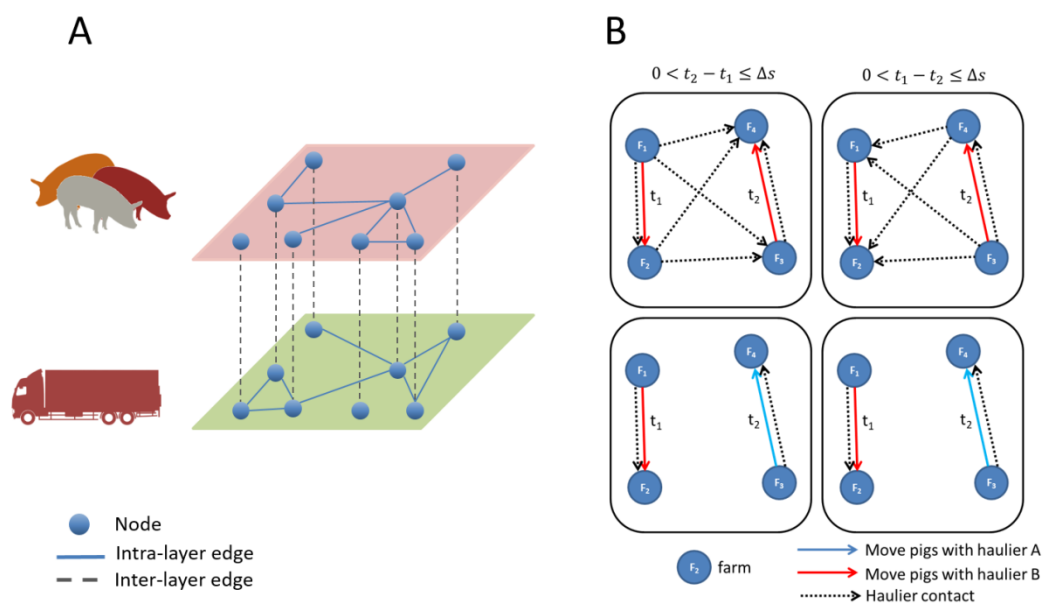
Figure 3. Structural changes of the weekly network topology when connection through private haulage companies (PHC) is and is not accounted for. Comparison in the distributions of nodes (A) in-degree, k_{in} , and (B) out-degree, k_{out} , for each premises (nodes) involved in moving pigs in each full week of the study period (i.e. $\Delta t = 7$) and for increasing values of contamination period, Δs , of PHC vehicles. (C) Proportion of isolated premises and (D) distributions of the size of the giant strong (GSCC) and weak (GWCC) component of the weekly pig trade networks for increasing value of Δs when defining PHC contacts. GSCC and GWCC are considered as proxy measures for lower and upper bounds of maximal epidemic size, respectively, for epidemics spreading in the considered network

Figure 4. Changes of the relative size of the giant components (GCC) with progressive targeted removal of nodes and when connection through private haulage companies (PHC) is and is not accounted for. Here, nodes were ranked in decreasing order of in-degree k_{in} , as computed over each monolayer network of direct contact and considering $\Delta t = 28$ days, and progressively removed from the networks. For all multilayer networks considered, the effect of the targeted removal of nodes was measured upon the relative size of the giant (A) strong (GSCC), and (B) weak (GWCC) components, expressed as a fraction of their size when no nodes were removed $GCC(0)$.

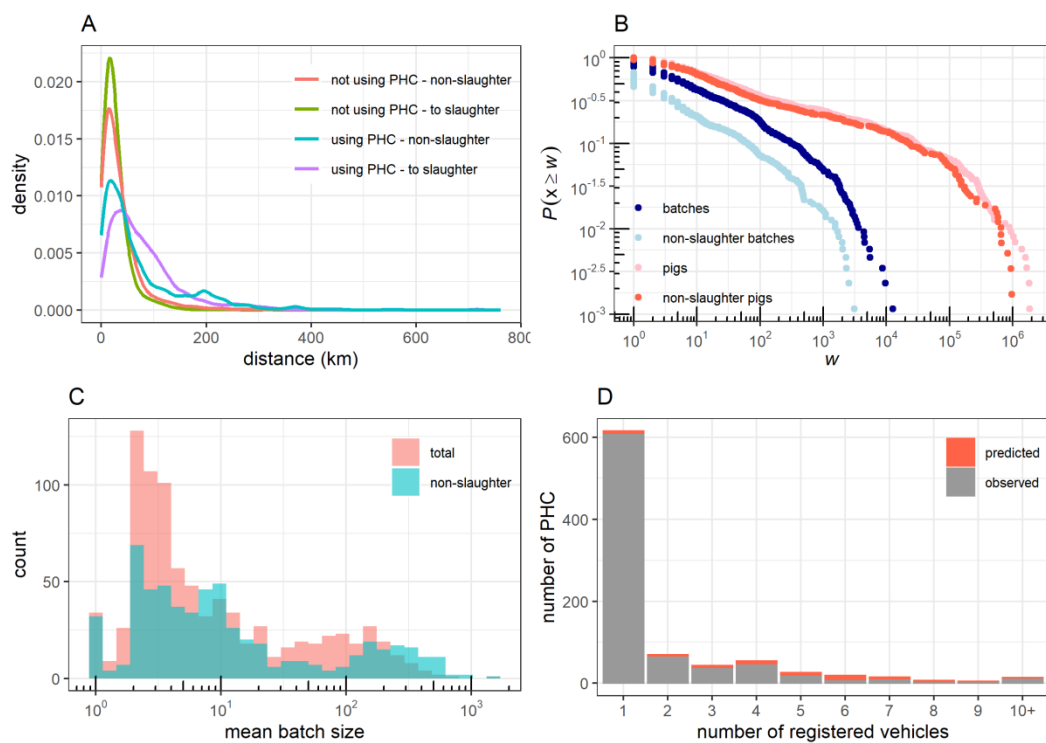
Figure 5. Threshold values inducing epidemic spread. (A-B) Line plot showing the evolution of the critical values of the transmission probability due to direct movements of pigs (β_M^*) that would raise the reproduction number R above 1 for increasing values of transmission probability due to the share used of PHC vehicles (β_H) and when contacts are aggregated over (A) $\Delta t=7$ days and (B) $\Delta t=28$ days. (C-D) Line plot showing the evolution of the critical values of the transmission probability due to the share used of PHC vehicles (β_H^*) for increasing values of transmission probability due to direct movements of pigs (β_M) and when contacts are aggregated over (C) $\Delta t=7$ days and (D) $\Delta t=28$ days. Here, we provide critical values for each considered scenario of contamination period of PHC vehicles (Δs).

Supporting information

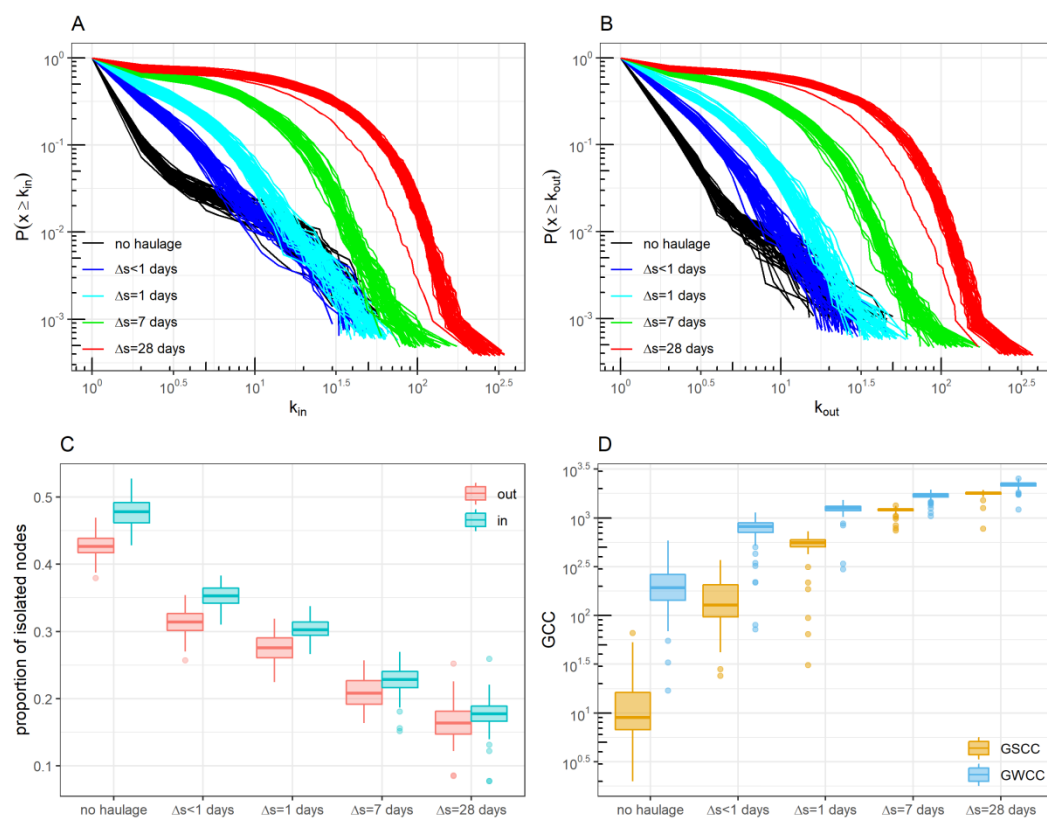
Supporting information S1. Supplementary Table and Figures.



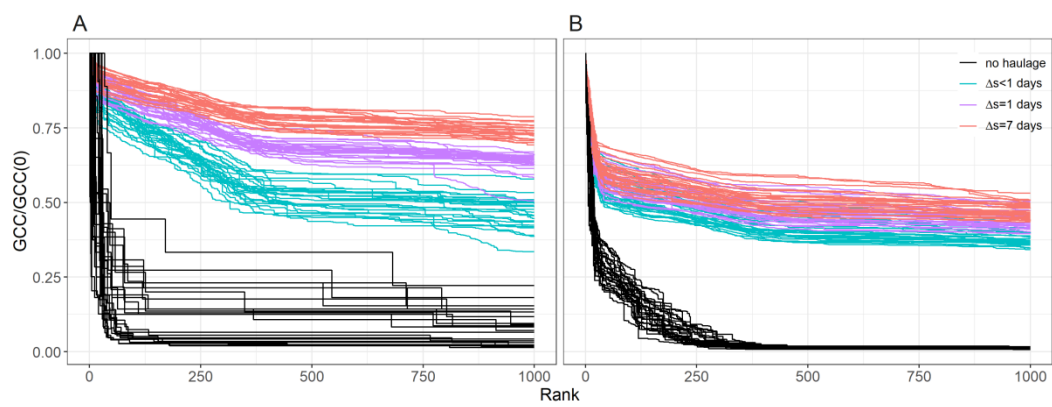
tbed_13459_f1.tif



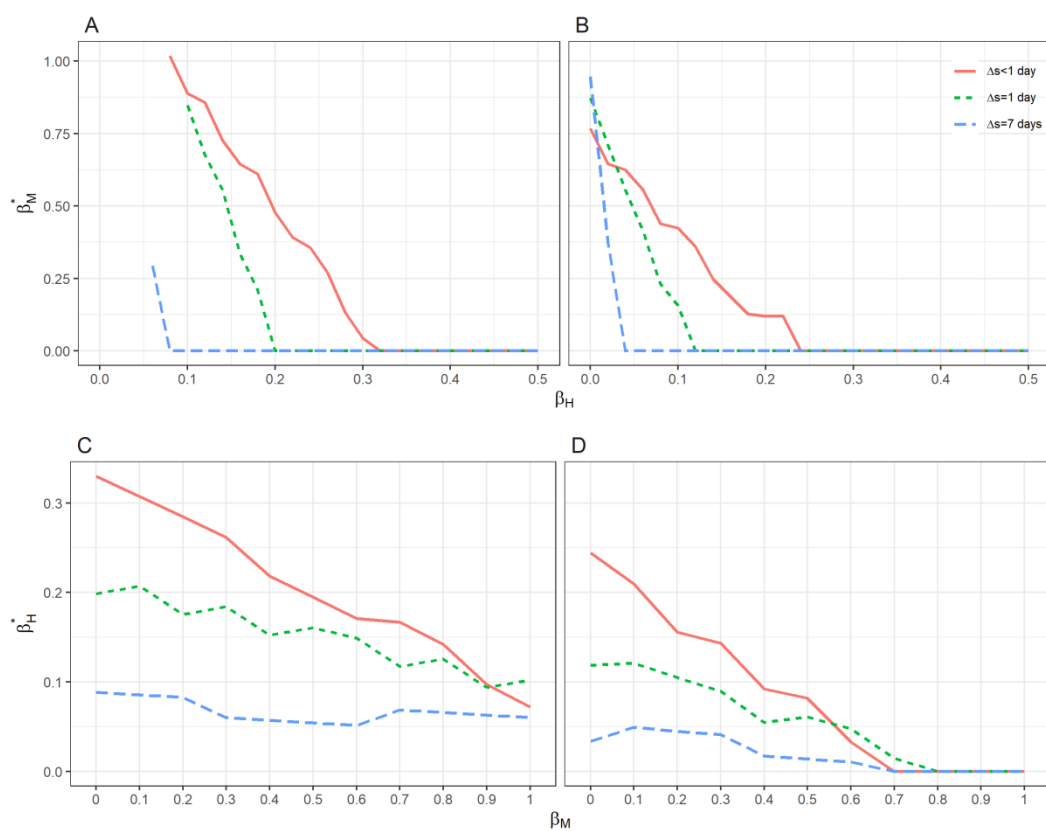
tbed_13459_f2.tiff



tbed_13459_f3.tiff



tbed_13459_f4.tiff



tbed_13459_f5.tiff